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BOOK REVIEW

Fossil Hominins: Neandertals

Neanderthals Revisited. New Approaches and Perspectives. Edited by Katarina Harvati and Terry Harrison. Dordrecht: Springer. 2006. 332 pp., $129.00 (cloth). ISBN 1-4020-5120-4

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In science, the more data available on a particular phenomenon, the more detailed and precise the questions articulated by scientists concerning those data and the phenomenon pertinent thereto. So it is with our close kin, the Neandertals. We know more about the Neandertals than we do about any fossil primate – perhaps any fossil vertebrate – "species." Not only do we have an excellent handle on their total morphological pattern, we also have a solid picture of their behavior (to the extent possible from fossils and archaeology), their developmental biology, and increasingly even their genome. *Neanderthals Revisited* aims to provide a current view of the questions being posed about Neandertals and an assessment of the plethora of data being generated to address those questions. Unlike the other top quality recent edited volume focusing on the "Neandertal question" (Conard 2006), *Neanderthals Revisited* deals exclusively with the biological issues, and this focus allows a more in-depth and broader consideration of those issues. Perhaps its most significant feature is the breadth of ideas and interpretations in the volume. Readers will gain an appreciation of the diversity of scientific perspectives on the Neandertals and their relationship to us rather than simply getting one side of the story. The result is an excellent and extremely useful compendium of approaches and perspectives, including some very novel ones.

Of the 17 original papers in the volume, two deal with the currently high-profile impact of genetic studies on understanding late Pleistocene human evolution, and these two illustrate well the diversity of perspectives on just what the genetic data can tell us. D. Serre and S. Pääbo review their findings based on ancient mitochondrial (mt) DNA and reiterate their previous conclusions that these data provide no evidence of introgression between Neandertals and early modern humans. They do note that low levels of gene flow are not precluded by these data, but the clear message is that these data show Neandertals to be substantially different from us. J. Hawks takes a very different view. He marshals evidence to demonstrate that mtDNA is not selectively neutral and argues that the modern-Neandertal difference may result from a recent "selective sweep" of human mtDNA. In stark contrast to Serre and Pääbo's confidence about the future contributions of genetic studies, Hawks (p. 221) posits that the impact of selection makes "Neanderthal mtDNA variation phylogenetically uninformative."

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The majority of papers deals with the interpretation of Neandertal morphology, and a diversity of methodologies and interpretations emerge. K. Harvati and D. Weaver compare cranial vault, facial, and temporal bone data among modern human populations, compared to genetic and climatic variables. They determine facial variation to be more climate related and that, while the other two morphological areas both correlated better with neutral genetic distances, temporal bone form was the better indicator of "genetic" relationship. Their assessment of Neandertal temporal bone patterns compared to the moderns lead them to the conclusion that Neandertals were a distinct lineage and thus, species. G. Bräuer and colleagues reach a similar conclusion about Neandertal-modern relationships based on multivariate and univariate metrical cranial analyses focused on the Mladeč early modern European sample. Interestingly, given the results of the previous Havarti/Weaver study, a significant part of this analysis focuses on the face. However, for both the face and the vault, Bräuer and colleagues find no evidence of Neandertal contribution. Several other papers focus on various aspects of Neandertal morphology (Tattersall/Schwartz, Bruner/Manzi, Niewoehner, Bailey/Hublin, Pearson and colleagues, Rosas and colleagues, Ponce de León/Zollikofer) and generally emphasize Neandertal distinctiveness. However, both Niewoehner (hand) and the Pearson group (upper limb) see the distinctions as primarily related to activity/behavioral differences. S. Bailey and J-J. Hublin focus on dental morphology to demonstrate that Neandertals produced the Châtelperronian at La Grotte du Renne (Arcy-sur-Cure) in France. This demonstration takes on particular importance given the recent assertion by O. Bar-Yosef (in Conard 2006) that the Neandertal-Châtelperronian association in France is suspect. Obviously, if Bar-Yosef is correct–and the Châtelperronian is produced by early modern people–current perspectives on modern human cultural and biological origins in Europe would be substantively altered.

Morphology-based studies by J. Ahern and J.-L. Voisin conclude that Neandertals and early modern people were capable of some degree of interbreeding. Ahern focuses on non-metric features and compares frequency differences in these traits between Neandertals and early modern humans with the differences between recent Amerindians and Euroamericans. He finds that the differences are not statistically significantly greater in the Neandertal-early modern human comparison than in the Amerindian-Euroamerican comparisons. He concludes that the hypothesis that Neandertals and early moderns represent the same morphospecies cannot be refuted with these data, but he goes on to question the utility of the morphospecies concept in evolutionary studies. It should be noted that Ahern's study focuses on morphological details rather than patterns of major morphological form. Voisin asserts that Neandertals underwent a speciation by distance, meaning that in the Near East Neandertals and early moderns were still capable of interbreeding as were populations of Neandertals and modern humans in the eastern part of Europe. However, the western European Neandertals had been isolated enough from non-Neandertal populations that they were likely not to have interbred with invading early modern populations. Similar morphological clines have been noted before for Neandertals, initially by F.C. Howell (1957) and then others, but Voisin's model certainly represents a very robust, novel approach.

The contribution by M. Ponce de León and C. Zollikofer stresses the importance of ontogenetic data to later hominin lineage divergence. They analyze craniofacial development from infant to adult in the two species of *Pan* compared to Neandertals and modern humans. They find that both lineage divergences (common chimpanzee/bonobo and Neandertal/modern human) are characterized by the latter form in each comparison exhibiting "abridged" spatiotemporal developmental patterns compared to the former, but the Neandertal/modern divergence appears to result from differences in prenatal developmental patterning whereas the

divergence in *Pan* is evident postnatally. In a second paper, Zollikofer and Ponce de León illustrate the usefulness of computer modeling in investigating the role of specific factors in changing developmental patterns. A. Rosas and colleagues also invoke developmental patterning in the origin of Neandertals. They suggest a two-phased model in which changes in ontogenetic dynamics of the skull produce the Neandertal morph and establish the Neandertal lineage as a distinct species.

In a unique approach to the role of climatic adaptation in Neandertal body form, S. Churchill revisits the idea that the large thoraces of Neandertals represent a cold adaptation. Using a bioenergetics approach and working with a half-size reconstruction of the La Ferrassie 1 male Neandertal, he determines that Neandertals had more elevated basal metabolic rates than previously thought. Churchill concludes that the expanded chests likely functioned more to fill the enhanced oxygen demand of the higher BMR than to provide strict adherence to Bergmann's rule. He also makes the point that higher energetic costs of thermoregulation in Neandertals may have reduced the energy directed to reproduction. This may provide a further rationale for explaining the relative rarity of Neandertals on the landscape. C. Stringer also examines the role of climate–in this case climatic instability–on the fate of the Neandertals. He sees such climatic factors playing a determining role in Neandertal extinction by providing a stressor that Neandertal populations could not adequately respond to. Stringer also notes the impact of more accurate dating on our picture of Neandertal-early modern interactions and suggests that Neandertals and early modern humans might well be best characterized as allotaxa.

Yet another novel and informative approach is provided by T. Holliday. He provides a discussion of the time it takes for mammalian species to achieve reproductive isolation, based on both molecular and paleontological data. As it turns out, the molecular and fossil evidence suggests minimum time spans of 1.4 million and 2 million years, respectively. Using a maximum estimate of Neandertal-modern human lineage divergence at ~700,000 years, Holliday concludes that they likely remained interfertile. There simply was not enough time since divergence for complete reproductive isolation to develop. However, he does assert that these two groups should still be considered separate evolutionary species and suggests that the dearth of evidence for interbreeding is that we either do not recognize it or that differences in appearance or behavior would prevent recognition of the other group as potential mates. From my perspective, I see Holliday's study dovetailing nicely with Voisin's model. It seems logical that geographic separation of populations could enhance the time effect. Thus, it may well be that interfertility would be less likely as one moves West, where Neandertals may have been the most isolated from non-Neandertal populations. But the bottom line is that both these studies, along with those of Ahern and Hawks, certainly challenge any attribution of reproductive exclusivity to the Neandertals.

As I hope this review reflects, *Neanderthals Revisited* provides very valuable contributions to our understanding of Neandertal biology and systematics. The fact that they do not all agree on the final conclusion of how Neandertals are related to us is an accurate reflection of the state of "Neandertal studies." The lay media's claims that Neandertals have been proven to be our cousins but not to have contributed to our ancestry are just not true. What is clear is that if Neandertals did contribute, it does not appear to have been a major contribution. Still it is not evident that such a contribution was as insignificant as some suggest. Regardless of how one views the evidence, *Neanderthals Revisited* is a fine volume that moves our understanding of these complex issues forward. I consider it a must read for anyone interested in any aspect of hominin evolution and believe it will stand for many years as the fundamental reference for the role of the Neandertals in our evolutionary history.

References

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